

LIFE HISTORY AND SOCIAL BEHAVIOR OF *ANELOSIMUS JABAQUARA* AND *ANELOSIMUS DUBIOSUS* (ARANEAE, THERIDIIDAE)

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ABSTRACT. The life history and social behavior of two sympatric spider species, *Anelosimus jabaquara* and *A. dubiosus* (family Theridiidae), were examined to provide comparative data of intermediate social behaviors in this genus of social spiders. Both species occur in sympatry in a subtropical humid lowland forest in Brazil and shared very similar life history traits such as univoltinism and slightly biased subadult sex ratios with more females per colony than males. Reproduction in *A. jabaquara* took place in early summer (December) and the brood developed during winter (April to October) under the care of females. But the reproductive periods in *A. dubiosus* and *A. jabaquara* were desynchronized by one month with *A. dubiosus* reaching maturity and mating in November. Both species showed cooperation in spinning and repairing the colonial web, in capturing prey and caring for the brood. When compared to *A. jabaquara*, in *A. dubiosus* there were 2.6× more individual spiders per colony, 1.4× more females than males, the colonial webs were 0.4× larger and the females showed greater cooperation in caring for the brood. We believe that *A. dubiosus* showed a more complex array of social behaviors when compared to *A. jabaquara* probably due to the greater tolerance of other conspecific individuals. We placed *A. jabaquara* in the same level of sociality as another non-territorial periodic-social species, *A. jucundus*. *Anelosimus dubiosus* would be a non-territorial permanent-social species in the same level of sociality as *A. domingo*, *A. rupununi* and *A. eximus*, but with less complex social behaviors than any of the former species.

RESUMEN. O ciclo de vida e o comportamento social de duas espécies de aranhas, *Anelosimus jabaquara* e *A. dubiosus* (família Theridiidae), que ocorrem em simpatria em uma floresta subtropical úmida no Brasil, foram estudados para fornecer dados comparativos de comportamentos sociais intermediários neste gênero. Ambas espécies possuem características de ciclo de vida muito similares, tais como: univoltinismo e razão sexual de subadultos ligeiramente desviada para mais fêmeas do que machos. A reprodução em *A. jabaquara* ocorre no início do verão (em dezembro) e a prole se desenvolve durante o inverno (de abril a outubro) sob o cuidado das fêmeas. Mas os estágios reprodutivos em *A. jabaquara* e *A. dubiosus* se encontravam desincronizados em um mês sendo que a reprodução em *A. dubiosus* se iniciou um mês antes—novembro—em relação à *A. jabaquara*. Ambas espécies mostraram cooperação na construção e reparo da teia colonial, na captura de presas e no cuidado à prole. Em *A. dubiosus* haviam 2.6× mais indivíduos por colônia, 1.4 mais fêmeas do que machos por colônia, as teias eram em média 0.4× maiores e as fêmeas mostraram maior cooperação no cuidado à prole quando comparada à *A. jabaquara*. Acreditamos que *A. dubiosus* tenha mostrado comportamentos sociais mais complexos quando comparada à *A. jabaquara*, provavelmente devido à maior tolerância de outros indivíduos da mesma espécie. Classificamos a espécie *A. jabaquara* como tendo um grau de socialidade similar ao de outra espécie não-territorial periódico-social *A. jucundus*. *Anelosimus dubiosus* foi classificada como uma espécie não-territorial permanente-social num grau de socialidade similar ao das espécies *A. domingo*, *A. rupununi* e *A. eximus*, mas com um grau de complexidade de comportamento social inferior aos das espécies anteriores.

Social behavior in spiders has originated independently in relatively few spider families (D'Andrea 1987, Avilés 1997). The existence of irregular webs that can be spun coopera-

tively by all individuals in a colony is an important preadaptation to the evolution of social behavior in spiders. This kind of web is typical for most the spider families that show

more complex social behaviors, such as Dictynidae, Agelenidae and Theridiidae. In such families another important adaptation would be the development of tolerance to conspecific individuals (Shear 1970).

The genus *Anelosimus* (Simon 1891) is of great interest because it contains solitary species as well as other species that show a gradient of social behaviors. This gradient is also exhibited in a few other species in the families Agelenidae, Dictynidae and Uloboridae; but *Anelosimus* has the largest number of social species known to researchers (Avilés 1997).

Avilés (1997) proposed a classification of social behaviors in spiders which is based on the length of time in which the spiders coexist as a colony (aggregation of individuals which live on the same nest and cooperate) and as to whether or not they maintain individual territories within the colony. Because spider species of the genus *Anelosimus* (Theridiidae) do not keep individual webs within a nest they can be grouped in two of the four categories: non-territorial permanent-social (quasisocial)—those species where “the adult members of a generation share a single communal nest and engage in cooperative prey capture and feeding”; non-territorial periodic-social (subsocial)—those species where “the siblings will continue to cooperate after the onset of maturity.”

The species *A. eximus* (Keyserling 1891) has been classified as non-territorial permanent-social (Avilés 1997) and represents the pinnacle of sociality in the family Theridiidae (Vollrath 1986). The most important characteristics of its social behavior are: overlapping of two or more generations that cooperate in web spinning, in web maintenance and cleaning, prey capture and brood care; extremely biased sex ratios towards females, non-cooperative males and the existence of non-reproductive females (Vollrath 1982, 1986). Their colonial webs can contain up to tens of thousands of individuals and reach an area greater than 50 m² (Brach 1975; Christenson 1984; Vollrath 1983, 1986). There are four other species of *Anelosimus* which show less complex social behavior: *A. domingo* (Levi 1963) (Levi & Smith 1982; Rypstra & Tiery 1989), *A. rupununi* (or *A. lorenzo*) (Levi 1979) (Fowler & Levi 1979), *A. jucundus* (O.P. Cambridge 1895) (Nentwig & Christenson 1986) and *A. studiosus* (Hentz 1850)

(Levi 1963). The key adaptation to the evolution of social behavior in this genus seems to be an increase in tolerance of conspecifics followed by overlapping of generations which would allow more complex social behaviors to develop.

We studied two other species in this genus, *Anelosimus jabaquara* (Levi 1957) and *A. dubiosus* (Keyserling 1891), which coexist in sympatry and show similar life cycles and social behaviors. Our objective was to document the life history and social behavior of these two species with the expectation that it would produce some comparable data to aid in unveiling the steps in the evolution of social behaviors within this genus. Since the life histories of these species were unknown our first step was to document their biology and social behavior. Next we compared their social behaviors to those of other social species in the genus based on the available literature.

METHODS

This study was developed in the mountain range of Serra do Japí, in Jundiá (23°11'S, 46°52'W), in São Paulo, Brazil. The colonial webs of both spider species occur on shrubs and trees of a subtropical humid lowland forest. Throughout this study we will use the word “colony” meaning the group of individuals that occupy a single web (colonial web) which was spun and maintained by these same individuals.

One trail of 1 km was marked at the elevation of 800 m and another at 1070 m above sea level. All the colonial webs found on these trails were individually marked in January and February of 1989. Measures of width, length and height were taken from each colonial web. Weekly observations were made, from January 1989 to March 1990, totaling 280 hours of field observations on the activity period of the colony, the number and stage of development of the spiders, the behaviors of web construction, prey capture and brood care.

One adult male and one female were collected from each colonial web for analysis of genitalia to distinguish between *Anelosimus jabaquara* and *Anelosimus dubiosus* (Levi 1963) and measured for the length of its cephalothorax. Voucher specimens were deposited in the Museum of Comparative Biology at Harvard University. We estimated the number

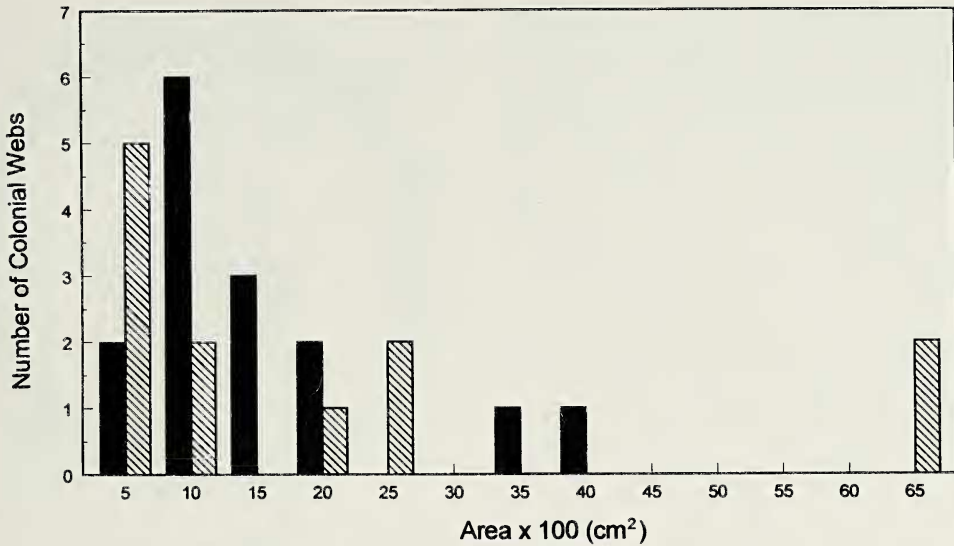


Figure 1.—Distribution of the sizes of the colonial webs of *Anelosimus jabaquara* (dark) and *Anelosimus dubiosus* (hatched) in the area of Paraíso I, Serra do Japí, Jundiá, S.P., Brazil in December 1989.

of individuals in a web by throwing a Diptera (Tabanidae) inside the web and counting the spiders as they came out to feed. Since there was only one generation of brood in a web in one year it was possible to also record the stage of development and sex if they were close to the adult stages. The plant support was collected and all plant species occurring on a transect of 1 km long and 10 m wide were also collected for identification.

In January of 1989 three large colonial webs, with detritus and containing the mature brood of one or more females, were collected from both species and taken to the laboratory where they were put on plants of the family Myrtaceae in an open terrarium (1 m × 1 m), for detailed behavioral studies which totaled 100 hours of observations and for determination of stages of their life cycle. The egg sacs and all the molts found in the web were collected. These spiders were fed the Diptera *Ceratitis capitata* (Tephritidae).

From November 1989 through January 1990, 51 colonial webs with detritus were collected in the field, 41 webs of *A. jabaquara* and 10 webs of *A. dubiosus*. These colonial webs were taken to the laboratory where they were dissected to determine the identity of every single individual in the web, the number of egg sacs, the mean number of eggs per egg sac and the sex ratio of adults. A short manipulative experiment was conducted in the

field on five large colonial webs with detritus of each of the two species. In these experiments one adult female of *A. dubiosus* was dropped onto the sheet of the colonial web with adults of *A. jabaquara* (replicated five times) and one adult female of *A. jabaquara* was dropped onto the sheet of the colonial web with adults of *A. dubiosus* (replicated five times) and the behaviors of all adult spiders involved were noted.

RESULTS

Web structure.—The web structure for both species was very variable, and therefore it was not possible to distinguish between the two species based on the web alone. The colonial webs of *A. jabaquara* were usually shaped as a sheet over the branches and incorporated the leaves of the supporting plant. This “sheet” was made of a dense mesh of non adhesive threads spun in various directions on the same plane. The sizes of the colonial webs ranged from 20 cm² to 4000 cm² (mean area = 1437.5 cm², $n = 16$) (Fig. 1). This sheet functioned as a protection against any intruding natural enemy coming from underneath the web. Above this sheet there was an area that was made up of the leaves of the supporting plant surrounded by loosely spun non adhesive silk threads, “the retreat”. The leaves served as shelter and the spiders were commonly seen hiding underneath these

leaves during the day. Above this area there were long adhesive silk threads spun vertically in the air and attached to the upper branches of the supporting plant; these were called the "threads to intercept prey" (see Brach 1975 for more details). The colonial webs of *A. dubiosus* were very similar to those of *A. jabaquara*, but usually the web was shaped as a basket instead of a sheet. The sizes of the colonial webs ranged from 100–6500 cm² (\bar{x} area = 2041.7 cm², $n = 12$) (Fig. 1).

Throughout this study we will be referring to two major types of webs: smaller webs, ranging in size from 1–150 cm², and characterized by new threads woven over green leaves and containing no detritus of any kind and the larger webs, ranging in size from 151–6500 cm², and containing considerable amounts of dead leaves and detritus. Approximately 88% of the colonial webs sampled were on plants of the family Myrtaceae while the frequency of occurrence of this plant family in this kind of vegetation was 15%. This was a significant difference and indicated a preference of these spiders for this family as a supporting plant for their webs ($G = 289.01$; $P < 0.001$; $n = 92$).

Life cycle.—*A. jabaquara* is a univoltine species with eight instars and the development of the colonies was synchronous. The reproductive period started in December and, at the population level, the first egg sacs were seen in the field in late January (Fig. 2). The spiderlings hatched and remained in the egg sac, going through their first molt inside the sac, sacs were present in the field for three months. The second and third stage or instar lasted one month each. The fourth instar, in the middle of the winter, lasted 3 months. The fifth instar lasted two months and with the arrival of the rains the sixth and seventh instar lasted approximately one month each. By early December the spiders had reached sexual maturity and started mating and caring for their egg sacs (Fig. 2).

Small colonial webs were originated by the dispersion of subadult individuals during the reproduction period and were easily identified in the field because these webs were always spun over the green leaves of the support plant and there were no detritus present in the form of dead leaves, dead prey or abandoned portions of web. The mean number of individuals on these new and smaller webs was 1.43 in-

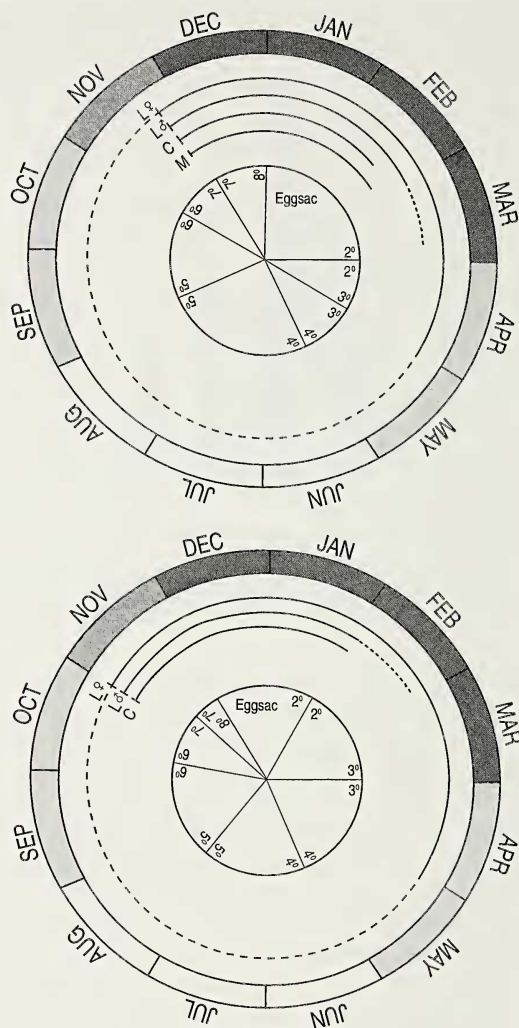


Figure 2.—Life cycle of the social spiders *Anelosimus jabaquara* (top) and *Anelosimus dubiosus* (bottom). The inner circle represents the duration of the life stages. The full lines represent the periods of copulation (C) and dispersion (M) and the longevity of males (L♂) and females (L♀). The outer circle indicates the rainy season (dark) and dry season (white).

dividuals per web ($SD = \pm 1.6$; $n = 32$) (Table 1). The larger colonies were at least one year old because that was the minimum time needed for all the detritus to accumulate. The mean number of spiders in these larger colonial webs was 29.11 individuals ($SD = \pm 20.26$, $n = 9$) (Fig 3).

Anelosimus dubiosus is also a univoltine species and showed a very similar life cycle to that of *A. jabaquara*, except that reproduc-

Table 1.—Composition of colonial webs resulting from dispersal of *Anelosimus jabaquara*, in December 1989, at Serra do Japi, Jundiá, S. P., Brazil. Females and males were present in subadult and adult stages of development.

Dispersing webs	Total number of individuals	Female	Males
1	1	1	
2	1	1	
3	1	1	
4	1	1	
5	2	2	
6	1	1	
7	1	1	
8	1	1	
9	1	1	
10	1	1	
11	1	1	
12	1	1	
13	1	1	
14	1	1	
15	1	1	
16	1	1	
17	1	1	
18	1		1
19	1		1
20	1	1	
21	1	1	
22	1	1	
23	1	1	
24	1	1	
25	1	1	
26	1	1	
27	1	1	
28	1		1
29	1		1
30	1	1	
31	1	1	
32	1	1	
Total	33	29	4

tion started one month earlier, in November, and the first egg sacs were recorded in December (Fig. 2). The duration of the instars varied when compared to those of *A. jabaquara* and the whole phenology was one month ahead in time. At the population level the early instars of *A. dubiosus* also showed a considerably longer period of time for development in the dry season (winter) when temperatures were lower (30 °C). Smaller webs were also present resulting from dispersion with an average of 2.2 individuals per web

Table 2.—Composition of colonial webs resulting from dispersal of *Anelosimus dubiosus*, in January 1989, at Serra do Japi, Jundiá, S. P., Brazil. Females and males were present in subadult and adult stages of development.

Dispersing webs	Total number of individuals	Female	Males
1	1	1	
2	1	1	
3	1	1	
4	1	1	
5	9	9	
6	1	1	
7	1	1	
8	1	1	
9	1	1	
10	1	1	
11	1	1	
12	1	1	
13	1	1	
14	1		1
15	1		1
Total	23	21	2

(SD = ± 3.29; $n = 15$)(Table 2). The mean number of spiders in the larger colonial webs was 86.5 individuals (SD = ± 56.45, $n = 6$)(Fig. 3).

Daily activity period.—The activity period for both species was similar. The spiders remained under leaves inside the retreat during the hottest hours of the day (from 1000–1500 h). They stayed in a resting position with their legs retracted under the cephalothorax. At dawn and evening the spiders gradually left the retreat and started renewing the silk threads in the web or position themselves on the threads above the retreat and waited for prey to fall. In cold and rainy days the spiders were active all day long. Prey capture occurred in the daytime if the prey vibrated enough to attract the spiders causing them to leave their retreats to capture the prey.

Reproduction.—The reproductive period in *A. jabaquara* started in December when new colonial webs of single individuals or of a few number of individuals were found in the field. Field observations showed that three individuals, two females and one male, were observed dispersing through the vegetation by throwing threads into the air; and once the

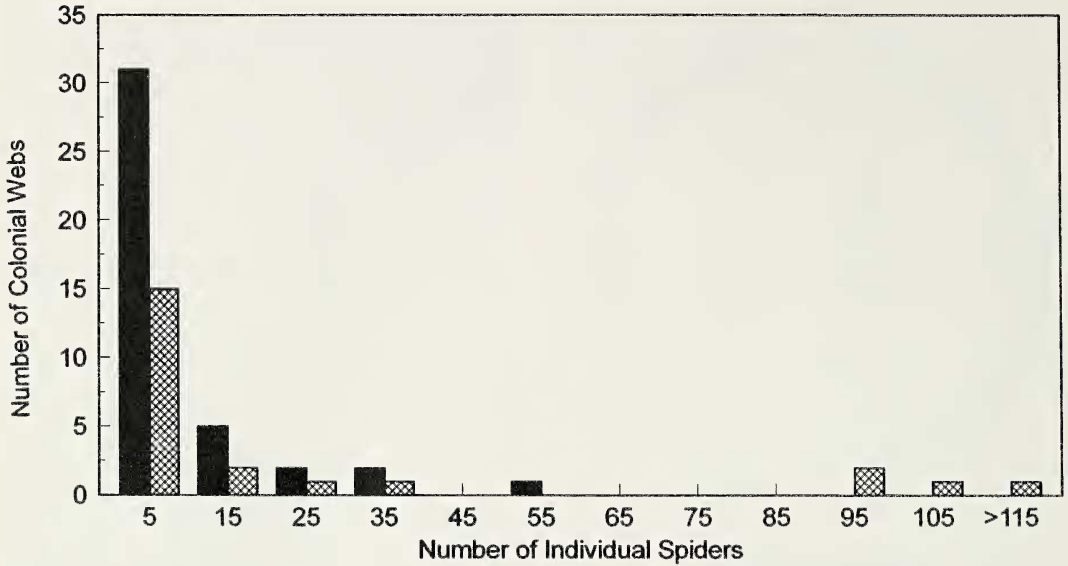


Figure 3.—Distribution of the number of individuals on colonial webs of *Anelosimus jabaquara* (dark) and *Anelosimus dubiosus* (hatched) in the area of Paraíso I, Serra do Japí, Jundiá, S.P., Brazil in December of 1989.

threads attached to the vegetation, they would move to the next plant (these individuals were identified as *A. jabaquara*). These new colonial webs resulting from dispersion of subadult and adult individuals were very small and contained only green leaves in its structure and no dried leaves or other detritus. Once these colonies were established the marked females did not seem to leave their web unless the webs were greatly damaged. But field observations showed that unmarked males and, less often, females were seen entering and leaving established new colonies during this period (two males and one female).

Laboratory observations showed that two marked females were seen copulating with more than one individual male from the same web and four marked males were seen copulating with different females. Field observations showed that a female that was caring for its egg sac was seen leaving the egg sac to copulate with a male.

In the three colonies reared in the laboratory each of the 24 females laid at least one egg sac with approximately 27 eggs ($SD = \pm 8.06$, $n = 34$) (minimum = 14 eggs; maximum = 49 eggs), being able to produce a second sac after abandoning their first. Approximately 25% ($n = 47$) of the egg sacs were unat-

tended and were either empty or had eggs parasitized by an unidentified microhymenoptera wasp. Other females that had their egg sacs experimentally removed tried to steal egg sacs from other females. Females that already had an egg sac or were caring for their brood were not seen laying a second egg sac.

Both in the field and in the laboratory females started dying in great numbers when their brood reached the 5th instar. Only one female survived until the brood reached the 7th or subadult instar. The males started dying soon after copulation and in January they were rarely seen in the field.

According to field observations the reproductive period in *A. dubiosus* started in November. Individuals of *A. dubiosus* were never found migrating in the field between webs, but we inferred that dispersion occurred because 14 small webs in the field contained single individuals and one small colonial web contained nine adult females (Table 3). In three larger colonial webs reared in terraria in the laboratory only one individual male of *A. dubiosus* ($n = 20$) dispersed and started a new web on a shelf, while all individuals ($n = 15$) of three colonies of *A. jabaquara* left the original web and dispersed, starting individual colonies on the shelves.

The males of *A. dubiosus* died in February

Table 3.—Composition of the sexes of colonial webs of *Anelosimus dubiosus* collected in the field from November (webs 1–5) and December (webs 6–10) of 1989, in Serra do Japi, Jundiá, S. P., Brazil.

Web #	Total number of individuals	Males	Females
1	18	4	14
2	17	4	13
3	15	0	15
4	10	6	4
5	104	34	70
6	18	4	14
7	20	8	12
8	12	1	11
9	20	2	18
10	95	15	80

and the females started dying when the brood was in the fourth instar. The mean number of eggs per egg sac in this species was 23.3 eggs ($SD = \pm 9.94$, $n = 38$) (minimum = 5 eggs; maximum = 47 eggs). Only one out of six larger webs had parasitized egg sacs (2 sacs out of 47 sacs) by an unidentified microhimenopteran wasp.

In March of 1989 a total of 54 smaller webs from both spider species and resulting from dispersion (sizes ranging from 1–150 cm²) had been marked and followed for 14 months. After 14 months 67% of the webs were abandoned and 17 of these colonial webs belonged to *A. jabaquara* and only one belonged to *A. dubiosus*.

Cooperation in brood care.—The males of *A. jabaquara* and *A. dubiosus* were not involved in brood care, probably because they were rarely present in the webs by then. Colonies collected in the field showed that adult males were usually smaller than adult females in *A. jabaquara* (mean male cephalothorax length = 1.38 cm, $SD = \pm 0.004$, $n = 24$; mean female cephalothorax length = 1.62 cm, $SD = \pm 0.005$, $n = 25$) as well as in *A. dubiosus* (mean male cephalothorax length = 1.4 cm, $SD = 0.174$, $n = 9$; mean female cephalothorax length = 1.64 cm, $SD = \pm 0.126$, $n = 12$). In both species the subadult sex ratio was biased towards females, in *A. dubiosus* it was 3.2:1 (females:males) (mean females per male per colony = 3.22, $SD = \pm 0.21$, $n =$

10) (Table 3) and in *A. jabaquara* it was 1.8:1 (females:males) (mean females per male per colony = 1.8, $SD = \pm 0.21$, $n = 42$) (Table 4). It was not possible to obtain the sex ratio of these spiders during the earlier stages of egg eclosion because the sex chromosomes in these species are microchromosomes and of difficult detection according to the Department of Cellular Biology of the University of Campinas.

In the field and laboratory, the females of *A. jabaquara* and *A. dubiosus* that were guarding their egg sacs moved very little and no new silk threads were added to the web during this period. The egg sacs were kept inside the retreat under leaves, and each female guarded its own egg sac.

Both in the field and laboratory the females of *A. jabaquara* rarely left the guard of their egg sac except when capturing prey or copulating and would return to their egg sacs immediately. The females inside their retreats could be as close as 10 cm from each other underneath different leaves or be touching each other while feeding. The females were very aggressive towards any conspecific female approaching its egg sac during reproduction. A female that was guarding its egg sac attacked any approaching female by touching the female with its front pair of legs, biting and pursuing it for a distance. A female, in the field, was seen gathering up to three other egg sacs besides her own under her retreat but when moving carried only one by the chelicerae. Another female, in the field, was seen feeding young spiderlings from a different brood (mother of the brood died) inside her retreat while caring for her own brood but that was only seen once.

Field observations show that spiderlings went through their first instar inside the egg sac. After they left the egg sac in their second instar they were gregarious staying with the female under a leaf in the retreat. The female showed the same protective behavior towards the brood as seen when it guarded the egg sac. The female fed her brood by what was believed to be regurgitation since the female would go to the retreat area and the spiderlings would all gather around the female's mouth area all at the same time. Four different adult females were seen feeding their brood by regurgitation until the spiderlings reached the third instar and were able to capture small

Table 4.—Composition of the sexes of colonial webs of *Anelosimus jabaquara* collected in the field from November (webs 1–12) and December (webs 13–41) of 1989, in Serra do Japi, Jundiá, S. P., Brazil.

Web #	Total number of individuals	Males	Females
1	60	27	33
2	57	31	26
3	14	8	6
4	31	14	17
5	34	14	20
6	45	25	20
7	55	19	36
8	47	5	42
9	41	16	25
10	32	9	23
11	39	16	23
12	40	3	37
13	59	33	26
14	23	13	10
15	35	10	25
16	22	14	8
17	14	9	5
18	71	59	12
19	10	5	5
20	89	42	47
21	21	6	15
22	56	19	37
22	11	5	6
23	49	21	28
24	27	14	13
25	47	21	26
26	40	19	21
27	17	11	6
28	21	12	9
29	11	6	5
30	42	18	24
31	17	7	10
32	35	18	17
33	78	35	43
34	46	27	19
35	12	4	8
36	20	11	9
37	20	10	10
38	18	10	8
39	18	11	7
40	12	8	4
41	35	8	27

prey on their own or would share the prey captured by the female. Around the fourth instar the juveniles of a brood mixed with those of other broods and the juveniles would either capture prey alone or in groups or eat prey captured by other females. Females started dying when the juveniles were in the fifth instar, while the males had died soon after copulation.

Field observations showed that the reproductive behavior of *A. dubiosus* was very similar to that of *A. jabaquara*, except that the females of *A. dubiosus* did not pursue the intruding females and were perceived as "less aggressive" towards each other and the broods of different females mixed in the second instar of their development. Each female of *A. dubiosus* guarded its own egg sac and would interact agonistically towards any approaching female by touching the front pair of legs and pulling the egg sac by the chelicerae. Intruding females were not pursued. In the second instar when the spiderlings had left the egg sac they mixed with spiderlings from other broods and any female in the web would feed the spiderlings by regurgitation. Older juveniles were also seen feeding the spiderlings by regurgitation. Females started dying when the brood had reached the fourth instar, while the males had died shortly after copulation.

Other social behaviors.—Both in the field and under laboratory conditions all the individuals, adult females and males (when present) and all spiderlings older than third or fourth instar, participated in the activities of web construction and repair, prey capture and occasionally removal of detritus. No significant difference was observed in the social behavior of the two species.

Web construction and repair: At dawn and evening all the individuals in the colonial web that were at the fourth instar or older in *A. jabaquara* and third instar and older in *A. dubiosus* left the retreat and started spinning silk threads in all directions with no apparent order. Some individuals started adding threads to the sheet while others spun threads at random over the retreat area. Still others spun threads up towards the leaves of higher branches. These individuals could switch activities anytime. This behavior enabled the spiders to add new threads to the web enlarging it as the individuals grew in size and also

to repair parts of the web that were damaged by rain, wind or animal activity.

Feeding behavior: In both species field observations showed that adult males and females participated in prey capture and that the bigger females (bigger abdomens) attacked the prey first by biting the thorax and abdomen of the prey. The smaller females (thinner abdomens) joined by biting the appendages or by turning their abdomen to the prey and releasing silk threads all over the prey with the aid of their last pair of legs. The females would then feed on the prey in groups or in the case of a smaller prey they would break the prey in parts and feed individually. After the prey had been immobilized by the females the males were seen biting the thorax and abdomen of the prey. The juveniles in their fourth instar helped the females in prey capture by biting the appendages of the prey. When the prey was not moving the juveniles would get on top of the prey and feed and the females would eventually abandon the prey, sometimes without even having eaten. The dead females were eaten by juveniles or other adult females in both species.

Removal of detritus: In both species the only objects removed by the spiders were empty egg sacs removed from the retreat area and thrown on the main sheet of the web.

Tolerance.—A short manipulative study revealed that when one adult female of *A. dubiosus* was dropped onto the sheet of the colonial web of adult *A. jabaquara*, the female at first would not move and when it moved it tried to escape from the web (all five trials). As soon as the individual of *A. dubiosus* moved, one or more females of *A. jabaquara* would approach and fight the intruding female, pursuing it until it had dropped from the web or had been killed. When one adult female of *A. jabaquara* was introduced in the web of adult *A. dubiosus* it would remain immobile for a few seconds and then go underneath a leaf; 30 minutes later two females were seen engaging in prey capture with the females of *A. dubiosus*, two others remained in the retreat and one dropped off the web.

DISCUSSION

The species *Anelosimus dubiosus* showed more complex social behaviors than its sympatric and conspecific species *A. jabaquara*. Both species showed the characteristics inher-

ent to other social spiders in this genus. They inhabited colonial webs with more than a few individuals, these colonial webs would survive for more than one year and the subadult sex ratio was biased towards females. Nevertheless, *A. dubiosus* had larger colonial webs, with almost three times more individuals per colonial web and the sex ratio was skewed for 1.4 more females per male in a colonial web when compared with *A. jabaquara*. Despite the fact that we used subadult sex ratios, the end result was that there were potentially more reproducing females on colonial webs of *A. dubiosus* when compared to webs of *A. jabaquara*.

The dispersion of subadults and adults early in the reproductive season was very costly with a 67% mortality rate after 14 months, for newly established webs. Both species showed dispersion of subadults and adult males and females early in the season and the mean number of individuals on these dispersing colonies was slightly higher for *A. dubiosus*. From a total of 58 webs established at the beginning of the season, after 14 months only 18 webs had survived, 17 of those were *A. jabaquara* and one web was *A. dubiosus*. It is still not clear if the main mode of dispersion of *A. dubiosus* happens by the dispersion of single individuals or by budding off the main colony. There was no information available as to the initial species composition of the webs resulting from dispersion, but fewer of these smaller webs found in the field belonged to *A. dubiosus*, and no individuals of this species were found migrating in the field. Because one dispersing web had nine females, it is possible that this species utilizes both dispersing strategies. Since the mode of dispersion is crucial information to the understanding of phylogenetic relationships and population dynamics of social spiders, more detailed information is needed on the dispersion of *Anelosimus dubiosus*.

The most striking behavioral difference between these two species was related to the greater tolerance and cooperation observed in the brood care behavior of females of *A. dubiosus*. In both species females guarded their egg sacs, probably to protect them against predation, but the females of *A. dubiosus* would not guard their brood once they had emerged from the egg sacs. The spiderlings of different broods mixed and females or older juveniles

were seen feeding any brood by what appears to be regurgitation. This greater tolerance of other adult females allowed greater cooperation among females in the care of the young spiderlings which could have resulted in larger colonies containing the broods of several females.

Females of *A. jabaquara* guarded their egg sacs, as well as their broods, until the third instar and showed greater aggressiveness towards other conspecific females during the reproductive period. Even though we could not distinguish between cannibalism and predation of egg sacs for both species, we hypothesize that the greater aggressiveness towards other conspecific females was used as a means of protecting the egg sac and brood from cannibalism as has been documented for other *Anelosimus* (Christenson 1986). As a result of this aggressiveness there was less cooperation among females, colonies were usually smaller and more often contained the brood of one or a few females.

Another intriguing fact is that even though *A. jabaquara* and *A. dubiosus* are sympatric species utilizing the same plant families as support plants for their colonial webs (probably due to the alternate position of the leaves) and with a significant dispersion of individuals during reproduction, these species rarely mix. In our field samples we never found individuals of one species in the other species' colonial webs. This could be due to the differences in timing of reproduction, or more likely, a result of their chemical signaling which is very well known as the means of communication in spiders. Entering the wrong web and not being recognized (chemically) as an individual from that colonial web would certainly mean that you would be a potential prey specially for females of *A. jabaquara* (Smith 1989; Nentwig & Christenson 1986).

According to Avilés' (1997) classification, *Anelosimus jabaquara* can be considered as non-territorial periodic-social because its colony sizes are small ranging from 1 to 55 individuals, suggesting that these colonies were probably the result of the offspring of one or maybe two females that matured and reproduced. The greater aggressiveness towards conspecific females and the intense dispersion suggests that the colonies consists mainly of siblings. Another periodic-social species with-

in the genus *Anelosimus* with similar life history and social behaviors would be *A. jucundus* (Levi 1963, 1976; Nentwig & Christenson 1986). *A. jucundus* showed many characteristics which are very similar to that of *A. jabaquara* such as: equal sex ratios, dispersion by subadult females and adult females, limited cooperation, aggression among females, one generation a year and usually smaller webs, even though a colonial web with up to 97 individuals was found (Nentwig 1986).

The colonies of *A. dubiosus* containing up to 176 individuals suggest that the brood of two or more cooperative females founded these colonies and therefore this species can be considered to be non-territorial permanent-social species. Based on Avilés's group selection hypothesis for permanent-social spiders we would expect *A. dubiosus* to have inbreeding isolated colonies much like the other permanent-social species. Even though this species has been shown to produce some migrating colonies of single individuals, these were few in number especially when compared with *A. jabaquara*; and there was also one new colonial web containing nine females which could be the result of budding off the main colony.

Anelosimus dubiosus had one characteristic in common with other non-territorial permanent-social *Anelosimus* species, *A. domingo* and *A. lorenzo* (Fowler & Levi 1979; Levi & Smith 1982): the greater tolerance among females and therefore greater cooperation in the activities of the colonial web. But the similarities end there because both *A. domingo* and *A. lorenzo* seem to have overlapping generations until the brood reaches adulthood, more than 1000 individuals per colony and sex ratios of up to 50 females per male. These characteristics resemble more those of *A. eximus* (Fowler & Levi 1979).

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